FUNCTIONAL MORPHOLOGY OF SOME FOSSIL PALAEOTAXODONT BIVALVE HINGES AS A GUIDE TO ORIENTATION

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Abstract. The dentition of some Lower Palaeozoic palaeotaxodontid bivalves is analysed; it is argued that variation in tooth form on the dental plate has a simple, direct relationship to the position of the hinge axis. In cases where the position of the hinge axis can be determined, the site of the ligament and the region of maximum opening of the valves may also be inferred. The ligament is taken to be posterior, and the region of maximum opening is regarded as anterior. A number of palaeotaxodontids are examined in the light of these suggestions.

In the absence of a pallial sinus, orientation of fossil palaeotaxodontid bivalves becomes a matter of subjective choice. Furthermore, the initial decision as to the orientation colours all subsequent descriptions of the taxon in question.

Various attempts have been made to overcome this problem, most commonly by reference to the morphology and orientation of surviving palaeotaxodontids, i.e. members of Nuculidae and Nuculanidae. Reference to the external ligament, invariably posterior in living forms, may also be made, but recognition of this feature is difficult where fossil material consists entirely of internal and external moulds. Such preservation is the rule rather than the exception in Lower Palaeozoic rocks. Driscoll (1964) has maintained that the position of accessory muscle scars in fossil palaeotaxodontid bivalves can be used to determine their orientation; but the success of this method also depends on good preservation, and often proves ineffective where correlation of the scars with those of modern forms is difficult. Since the forms being considered in this paper are Palaeozoic, anything from 300 to 500 million years may have elapsed since their fossilization, and hence such analogies with living taxa are at best tenuous.

The use of a single morphological feature to determine the true orientation of fossil palaeotaxodontid bivalves would seem unreliable, and the use of several features might provide a sounder basis for determination. It is the purpose of this paper to suggest the use of the dentition, in conjunction with the pattern of musculature, etc., as a primary means of orientation of fossil palaeotaxodonts. However, it should be stressed that the use of the dentition is only suitable when the teeth along the dental plate show variation in both shape and size.

The morphology of the dentition

Marked variations in the shape and size of teeth along a single palaeotaxodont hinge were first observed in a well-preserved Ordovician (Llandeilo) fauna from Finistère, France (Bradshaw 1970). Further work shows similar variations in specimens from the Lower Devonian of New Zealand.

In the Ordovician forms the dental plate is constructed of two main sections, one on either side of the umbo, and usually arranged at an angle to each other. The dentition

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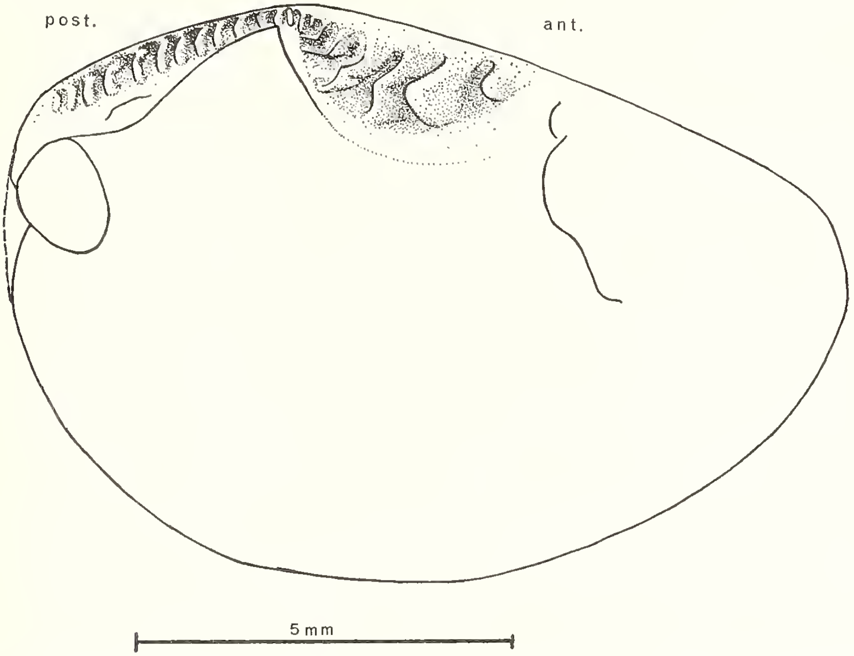
may either bridge the junction of these sections continuously, or the two sections may abut against each other discontinuously. The two dental sections bear teeth that are different in both shape and size, one section having large chevron-shaped teeth (later argued to be anterior), the other much lower ridge-like teeth (later argued to be posterior) (text-fig. 1).

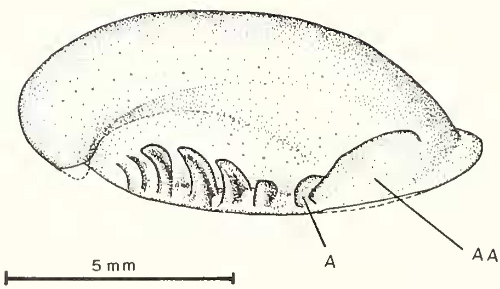


TEXT-FIG. 1. Detail of the hinge region of a right valve *Praeleda costae* to show the different character of the teeth on each side of the umbo. Specimen O.1, Middle Ordovician, Finistère.

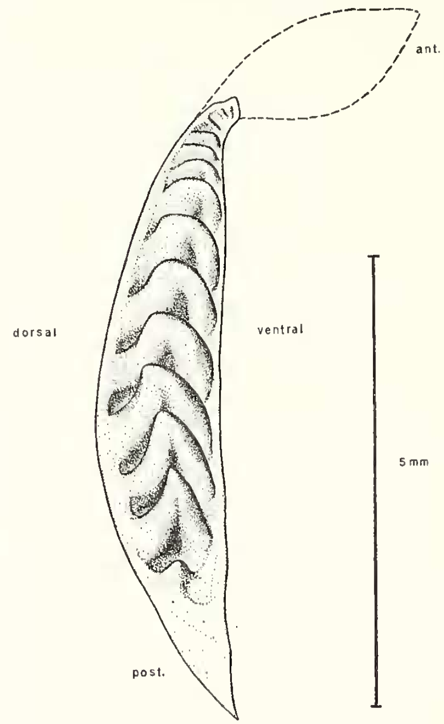
The larger teeth show a marked increase and decrease in size, with highest teeth near the centre of the row. Each tooth has a strong groove on the side facing away from the umbo, and the chevron is directed towards the junction of the two dental sections. When viewed along the axis of the dental section the teeth are not symmetrical, but are curved, with the ventral edge convex and the dorsal edge concave, the groove following this curvature (text-figs. 2, 3). This curvature of the tooth is in a plane which is not perpendicular to the axis of the dental section in which the tooth lies. The teeth on the other dental section have either a low symmetrical chevron form, or an angulated shape with a ventral limb so much longer than the dorsal that the tooth appears ridge-like. Such ridge-like teeth can sometimes be seen to pass gradually to more symmetrical teeth along a single dental section (text-fig. 3).

The mechanics of valve opening

(*a*) *Theoretical.* A general account of the mechanics of hinging of the bivalve shell can be found in Trueman (1964). In palaeotaxodontids with an angulated dentition composed of two distinct dental sections, such as the genera discussed here, the hinge axis, i.e. the theoretical axis about which the valves rotate during opening, must correspond to one or other of the dental sections, or else lie somewhere between them (text-fig. 4).



TEXT-FIG. 2



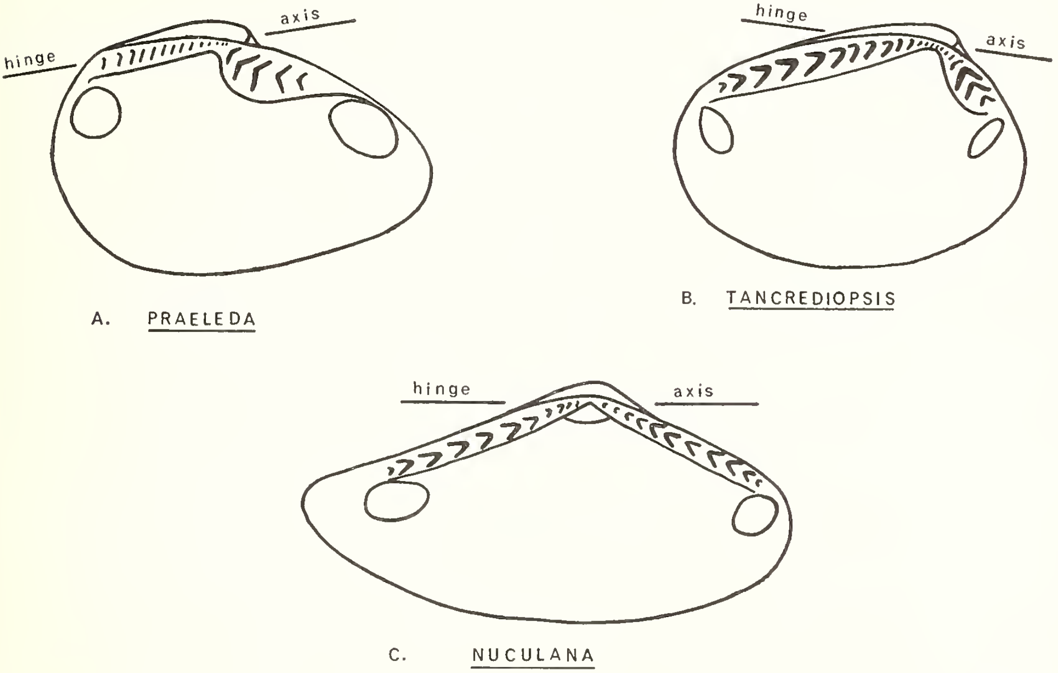
TEXT-FIG. 3

TEXT-FIG. 2. Left valve of *Praeleda* showing the curvature of the long anterior teeth. AA—anterior adductor muscle scar. A—anterior accessory muscle scar. Specimen A.20, Middle Ordovician, Finistère.

TEXT-FIG. 3. The posterior dental section of *Tancrediopsis ezquerrae*, with the outline of the anterior dental section indicated. Unlike *Praeleda* the teeth of this genus are more similar in size and shape along the dental plate. Those to the posterior reach the same height as those to the anterior but are more numerous (see text-fig. 4B for entire dental plate). The teeth of the posterior section grade from a large curved chevron-shape distally, to low ridges close to the umbo. The low ridges suggest proximity to the hinge axis and the external ligament is thought to coincide with this part of the dental section. Specimen A.9, Middle Ordovician, Finistère.

Where the hinge axis coincides with one dental section, the function and movement pattern, and consequently the appearance of the two series of teeth, will be quite different. During opening all teeth will move along curved paths centred on the hinge axis. The further a tooth is from the hinge axis the greater will be the influence of the arcuate movement path on tooth form. It is suggested that teeth near the hinge axis would be either low and rounded or ridge-like and set at right angles to the axis. Teeth distal to the axis would be much higher, so that their tips might remain engaged during maximum opening, and would be conspicuously arcuate about the axis, with curved faces or edges, depending on their exact orientation. The two blade-like limbs of a chevron tooth would have curved faces and an arcuate junction, all concave towards the hinge axis.

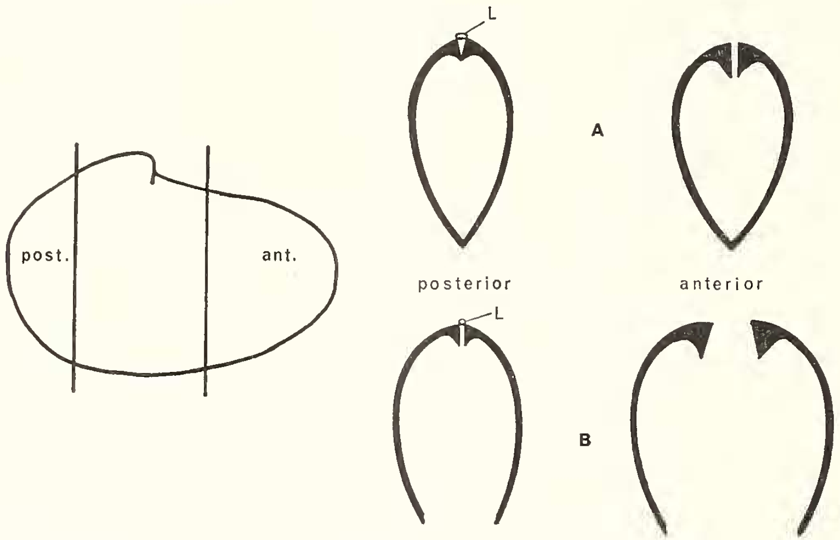
(*b*) *Examples*. The predicted pattern corresponds well with that found in many palaeotaxodontids. The long arcuate teeth of *Praeleda* (text-figs. 1, 2) could not have been situated near the hinge axis, since any type of pivotal action would have fractured them, unless the corresponding sockets were much larger. There is no evidence to suggest this, the teeth and sockets appearing identical in size.



TEXT-FIG. 4. Diagrammatic representation of A, *Praeleda*, B, *Tancrediopsis*, and C, *Nuculana* (all left valves) to show the variation in dentition and its relationship to the inferred hinge axis.

If it is accepted that the valves were most widely separated along the dental section bearing the highest teeth, then it follows that there could have been no external ligament above this section, and that the ligament must have been either concentrated near the umbo, or, more probably, dorsal to the shorter-toothed dental section.

Genera (e.g. *Tancrediopsis*, text-fig. 4B) in which the hinge axis coincides with neither dental section, show intermediate characters, with different tooth types on the same dental section. Genera (e.g. *Nuculana*, text-fig. 4C) in which the dental sections were equally displaced from the hinge axis have two symmetrical rows of teeth on either side of the umbo. The position of the ligament may be also inferred from the disposition of the surfaces of each dental section to the commissural plane. In text-fig. 1 the plane of the section bearing the largest teeth is parallel with that of the commissural plane, whereas that of the narrower section is at an angle to it. The two sections merge below the umbo. This difference appears directly related to the functioning of a ligament immediately above the narrower dental section. It will be obvious that when the valves are closed the surfaces of the wider dental section will be parallel and closely applied. By contrast, those of the narrower sections will be dorsally divergent. The relative positions of these two surfaces will ensure that the ligament is under tension (text-fig. 5).



TEXT-FIG. 5. Schematic sections through *Praeleda* to show the differing relative positions of the anterior and posterior dental sections when the valves are A, closed and B, open. When the valves are closed the posterior dental sections are dorsally divergent and the anterior ones parallel. When the valves are open the posterior dental sections become parallel and the anterior ones dorsally convergent. The vertical lines are the lines of section. L—ligament.

With relaxation of the adductor muscles and opening of the valves the tension in the ligament is reduced. The ligament decreases in width and the surfaces of the narrower dental section become parallel so that the entire surface is engaged. At the same time the surfaces of the wider dental sections become dorsally convergent.

Fossil examples

Cardiolaria beirensis is an Ordovician bivalve with a well-differentiated dentition (Bradshaw 1970, text-figs. 2, 3, 4). The largest teeth, which are curved and chevron in shape, are situated on the shorter side of the valve, suggesting that this genus has a 'normal' orientation. This assumption is further reinforced by the musculature of *Cardiolaria beirensis*. The anterior scars are deeply impressed, the adductor muscle being strengthened posteriorly by a sturdy myophoric plate. The three adjacent accessory muscle scars are analogous with the anterior protractors and anterior retractor muscles of the modern *Acila divaricata* and confirm that the shorter side of *Cardiolaria* is anterior. The anterior teeth are fewer than those on the longer posterior section which are chevron to ridge-like in form and smaller in size.

Praeleda costae and *Praeleda ciae* are Ordovician bivalves with well-differentiated dentitions. In this genus large, strongly curved teeth are found on the extended side of the valve and low ridge-like teeth on the shorter side, suggesting a 'reversed' orientation (Bradshaw 1970, text-figs. 7–12).

Deceptrix carinata from the Lower Devonian of Germany has a dentition very similar to that of *Praeleda costae* (see McAlester 1968, pl. 6, figs. 1–10), although its general shape is more symmetrical. In both these genera the hinge axis is suggested as corresponding to a major portion of the posterior dental section (text-fig. 4A).

Tancrediopsis ezquerrae is an Ordovician species in which, although the two sections are of unequal length, both contain large chevron teeth at their distal ends, grading into low teeth towards the umbo (text-fig. 3). It is suggested that the hinge axis no longer coincides with one dental section as in *Praeleda*, but is removed to a position parallel to a line between the adductor muscle scars (text-fig. 4B). The abrupt change in tooth character in the 'anterior' section (Bradshaw 1970, text-fig. 5) results from the rapid convergence of this section with the hinge axis; and conversely, the slow change in the 'posterior' teeth indicates a less strong convergence of this section. Lines between teeth of similar geometry would parallel the hinge axis. Comparison with the geometry of other forms suggests that the longer side is posterior. In some ways this species could be thought of as approaching the geometry of *Nuculana*.

In *Nuculanella* sp. of the New Zealand Lower Devonian the dental sections are equal in size and the teeth on them similar in number. Both series of teeth are chevron-shaped and curved, and the dental plate is interrupted by an internal ligament that would require a hinge axis almost equally displaced from each dental section.

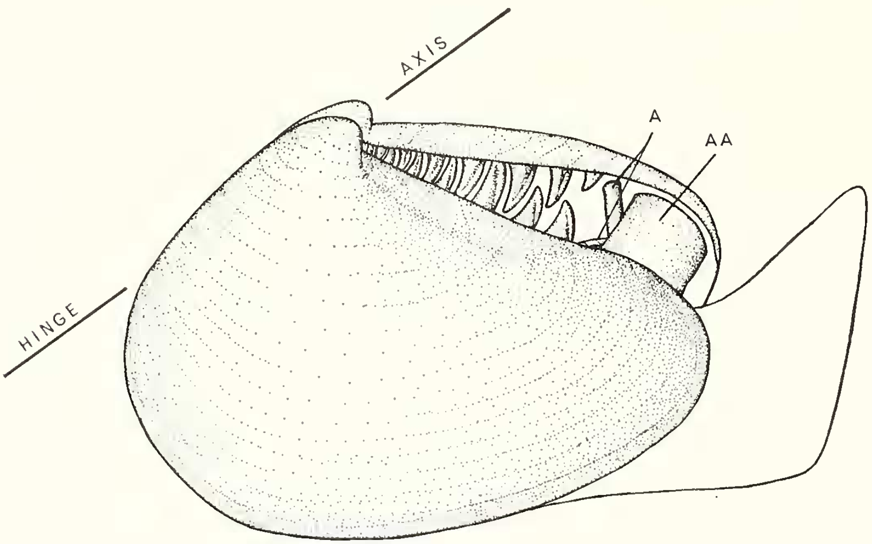
In *Culunana* sp. of the New Zealand Lower Devonian an internal ligament is clearly visible, but unlike *Nuculanella* sp. the dentition is well differentiated into two uneven series, although the smaller-sized teeth are not as low or ridge-like as those seen in either *Praeleda* or *Deceptrix*. *Culunana* sp. may well represent an evolutionary stage half-way between forms with a truly external ligament and differentiated teeth (e.g. *Praeleda* and *Deceptrix*) and those with a truly internal one and a uniform dentition (e.g. *Nucula*, *Nuculana*, and possibly *Nuculanella*).

Anthraconeilo taffiana, a Carboniferous bivalve well illustrated in McAlester 1968, pls. 18, 19, possesses a distinct pallial sinus indicating that the genus has a normal orientation. The longer, posterior side of the dental plate is straight and bears many regular teeth, distinctly chevron at the distal end of the series, but more assymetrical and ridge-like towards the umbo, showing similarity to the posterior series of *Cardiolaria beirensis*. The short, anterior dental section is wide and bears a few, large teeth that show rapid increase and decrease in size (see especially pl. 18, fig. 1). Paratype D, an articulated internal mould (pl. 18, fig. 2) clearly shows a curved profile to the anterior teeth. The geometry of the dentition independently suggests a normal orientation, with a hinge axis coincident with the lower teeth of the posterior section, and an external ligament immediately dorsal to them.

General conclusions

By reference to the burrowing action of modern palaeotaxodonts the authors suggest that the largest teeth on a differentiated dental plate of a fossil palaeotaxodont are most likely to be situated on the anterior dental section.

Observations by Yonge (1939) show *Nucula* to be a shallow burrower, resting with the anterior margin of the shell parallel with the sediment surface, and being covered by approximately 1 mm of sediment when buried. He describes in detail the action of burrowing by *Nucula nucleus* (Linné). After first being extended ventrally into the sediment, the closed foot is moved anteriorly and outwards. The two halves of the sole then open out widely to anchor in the sediment, and by the contraction of the pedal retractors the animal is pulled down and forwards. The foot is finally withdrawn between the



TEXT-FIG. 6. Interpretive reconstruction of the opened valves of a *Praeleda*-type bivalve to show how a hinge axis coincident with the low ridge-like teeth would give rise to a large opening at the inferred anterior, and would require large teeth along that side. The anterior adductor muscle—AA, and the accessory muscles—A, are shown, together with the possible position of the extended foot.

anterior margins of the shell after which the soles come together once more. It is significant to note that a large amount of anterior opening between the two valves is necessary to allow the large, extended nuculoid foot to be withdrawn into the shell. When resting and feeding below the surface only a small anterior and posterior opening is necessary to allow a slow current to pass through the mantle cavity.

As already indicated, the large curved chevron teeth of many palaeotaxodont bivalves suggest a relatively large degree of opening between the dental sections that bear them. It seems probable that this opening was necessary to accommodate the protrusion and retraction of a large active foot similar to that of modern forms (text-fig. 6), but that the opisthodetic ligament required a different type of dentition to that of *Nucula*.

Summary

1. Marked variations in size and shape of the teeth are visible on the hinge plates of Palaeozoic palaeotaxodontids, but have not been observed in modern forms. In this differentiated dentition the anterior dental section bears large, well-shaped, curved

chevron teeth, whereas the posterior section possesses low rounded teeth, chevron to ridge-like in form.

2. The curvature of the large teeth is centred on a projection of the part of the adjacent dental section that bears the lower teeth, and this line is considered to be the hinge axis.

3. In detail the shape of the teeth is governed by their orientation and position with respect to hinge axis. In order for the valves to open, those adjacent to the hinge axis must be low or ridge-like. Those furthest from it must be long and curved.

4. Forms with an internal ligament possess teeth that are more uniform in shape and size since the hinge axis is more symmetrically placed to the dental sections than is the case with an external ligament.

5. By reference to modern active palaeotaxodonts, the degree of opening suggested by the long curved teeth is considered to be anterior, necessitated by the size of the foot during retraction. This suggestion is supported by reference to the musculature and pallial lines of some palaeozoic palaeotaxodonts.

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